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# Biology of the Percids

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*Key words*: Percidae, structure, origin, biology, morphology, systematics, migration

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Les auteurs passent brièvement en revue la structure, l'origine et l'étendue de la famille des Percidae et comparent ses caractéristiques avec celles d'autres familles de poissons d'eau douce.

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[1]This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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Ils suggèrent que les percidés, essentiellement fluviatiles, ont vu leur succès entravé en Amérique du Nord par la présence des Centrarchidae. Les percidés sont définis comme poissons mésothermes tempérés, et on démontre que cette caractéristique physiologique, couplée à une capacité osmorégulatrice et à une performance de nage, limite les aires des perches. Le degré de développement du tapis réflecteur chez *Stizostedion* spp. et de la ligne latérale chez tous les percidés est lié à des différences dans le développement, le comportement alimentaire et l'habitat. Les auteurs passent également en revue le comportement reproducteur, alimentaire et migratoire.

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THIS paper reviews important morphological characters of the family and summarizes available information on the biological processes of reproduction, feeding, and migration. An attempt is made to provide a general overview of the family and then to concentrate on the species of most interest to PERCIS — members of the genera *Stizostedion*, *Perca*, and *Gymnocephalus*.

*Composition and origin of the Percidae* — The Percidae, with about 163 species, is a basal percoid freshwater fish family that resembles the Centrarchidae and the Cichlidae and differs from the Serranidae and Percichthyidae and many other familes of marine percoids in the absence of a subocular shelf and in having one or two instead of three anal spines. The Percidae differs from most other percoid families in having one or no predorsal bones instead of two or more. The anatomical characteristics of the family are summarized by Collette and Bănărescu (1977). The family is divisible into two subfamilies (Collette and Bănărescu 1977): the Percinae, which have large anal spines and a well-developed anteriormost interhemal bone, and the Luciopercinae, which have the anal spines poorly developed and the interhemal bones of uniformly small size. In each subfamily parallel evolution has led to mostly small, benthic, rheophilic forms with terete or depressed bodies and reduced or vestigial swimbladders. This differentiation is reflected by recognition of two tribes in each subfamily. Within the Percinae, the Etheostomatini (the three genera of North America darters) are interpreted as derivatives of the Percini (*Perca*, *Gymnocephalus*, and *Percarina*). Within the Luciopercinae, the Romanichthyini (the European *Zingel* and *Romanichthys*) have evolved from the Luciopercini (*Stizostedion*).

The Percidae appears to have originated from some anadromous basal percoid family during the Cenozoic in Europe, spreading to North America through at least two separate invasions. A critical review of available fossil material (*Amphiperca*, *Anthracoperca*, *Leobergia*, *Plectropoma*, *Propercarina*) is needed not only to provide information on paths and times of movements but also to help interpret evolutionary trends within the family.

*Evolutionary characteristics of Percidae and other freshwater fishes* — Before proceeding with the morphology and biology of the percids, we consider briefly some phylogenetic and historical factors that have influenced the distribution and evolution of primary freshwater fishes. We follow Myers' (1938) definition of primary freshwater fishes as those groups of fishes restricted to freshwater and whose evolution has taken place in freshwater. Of the approximately 21,000 species of living fishes (Cohen 1970), an astonishingly high 41.2% live in freshwaters, which constitute only about 0.0093% of the total water area of the world (Horn 1972). Most freshwater fishes are relatively primitive, soft-rayed (malacopterygian grade) fishes that differ from more advanced, spiny-rayed (acanthopterygian grade) fishes in a series of characters including the following seven, which are of evolutionary importance:

| Character | Malacopterygii | Acanthopterygii |
|---|---|---|
| 1. fin rays | soft rays | some true spines |
| 2. scales | cycloid | ctenoid |
| 3. pelvic fin position | abdominal | thoracic (or jugular) |
| 4. pelvic fin rays | more than 5 | 1 spine and 5 rays |
| 5. maxilla | included in gape | excluded from gape |
| 6. swimbladder | physostomous (connected to gut) | physoclistous (not connected to gut) |
| 7. dorsal fins | 1 (sometimes followed by adipose fin) | 2 (sometimes joined) |

These evolutionary advances confer selective advantages on the acanthopterygian fishes in manoeuvrability (1, 3, and 7), protection against predators (1, 2, and 4), maintenance of contact between the sexes in spawning (2), more efficient

feeding (5), and the ability to colonize relatively deep waters (6).

The largest component of primary freshwater fishes is the superorder Ostariophysi, which includes about 6000 species (catfishes, minnows, loaches, characins, and their relatives). They have two important adaptations that have aided them in retaining dominance over the freshwaters of the five major continents: the Weberian apparatus, a chain of small bones that links the inner ear with the swimbladder thereby increasing their hearing ability and an alarm substance (Schreckstoff) that warns other members of their species when an individual is wounded by a predator (Pfeiffer 1967; Rosen and Greenwood 1970; Roberts 1973). Many ostariophysans have a low oxygen demand and a high tolerance of elevated $CO_2$ concentrations.

Although spiny-rayed (acanthopterygian) fishes dominate many marine areas such as coral reefs, several families have successfully invaded freshwater. The three most successful freshwater percoid families are the Cichlidae (South America and Africa), Centrarchidae (eastern North America), and Percidae (temperate waters of the northern hemisphere). The Centrarchidae and Cichlidae are primarily laterally compressed fishes adapted for life in lakes. The Percidae, however, lack specific adaptations to lacustrine life and appear to have diverged less from their anadromous ancestors. Kitchell et al. (1977) discuss the riverine nature of percids at greater length. Presence of the Centrarchidae in eastern North America may have been a factor in limiting the number of large percids to three, the yellow perch (*Perca flavescens*), the walleye (*Stizostedion vitreum*), and the sauger (*S. canadense*). Five comparable species, the perches *P. fluviatilis* and *P. schrenki* and the pikeperches *S. lucioperca*, *S. volgense*, and *S. marinum* occur in Europe, where the absence of the Centrarchidae may have been a factor that permitted their evolution and that of the four moderate-sized percids of the genus *Gymnocephalus*.

*Limits to ranges* — Ranges of percids are limited by three main factors. Two are common to all primary freshwater fishes — highlands physically separating the upper parts of different river systems, and salt water physiologically preventing movements from the lower part of one river system to the next. In addition, percids are limited by high summer temperatures. They are adapted to temperate climates of the northern hemisphere where temperatures range from <4°C for more than 8 mo in northernmost latitudes to about 32°C in southernmost extremeties of their native range. Physiological optima vary from 22 to 28°C and ultimate upper incipient lethal temperatures from 29 to 35°C for those species that have been tested (Hokanson 1977).

The best data available on the thermal and salinity limits to percid distribution are for natural and introduced populations of *P. fluviatilis* and *P. flavescens*. Evidence from introductions of *P. fluviatilis* to Australia has been used to develop concepts concerning factors limiting the range of this species and of *P. flavescens* in their respective ranges in Eurasia and North America (Weatherley 1963, 1974, 1977; Weatherley and Lake 1967).

Thermal preferenda for these two percid species, and others also, compared with their upper lethal temperatures, suggest that in many parts of their ranges they would avoid dangerously high temperatures when possible (Hokanson 1977). High winter temperatures may also retard maturation and damage oocyte formation in *Perca* spp. (Weatherley and Lake 1967; Hokanson 1977). However, near the edges of their ranges at certain points, especially in Italy, central USA, and Australia, high temperature may act fairly directly to limit range extension (Weatherley 1963, 1977; Hokanson 1977). Willemsen (1977) reported a somewhat higher lethal temperature (33.5°C) for *P. fluviatilis* than others have found and McCormick (1976) has found a similar upper lethal temperature in *P. flavescens*.

Perch can tolerate salinity of up to 10‰ (Driver and Garside 1966; Privolnev 1964). As Thorpe (1977a) noted, this enables them to survive in the Baltic and Aral seas, and Chesapeake Bay, but it also means that they are unable to extend their present range by sea coastal movements to new river mouths (Weatherley 1974, 1977). Other species of percids (except *S. marinum* and *Percarina demidoffi*) have been less salinity tolerance and so are restricted to strictly freshwater.

## Morphology

*Swimbladder* — The swimbladder is an important structure that enables many species of bony fishes to be neutrally buoyant, thereby allowing them to rest motionless in midwater. Members of the two most primitive tribes of the Percidae, the Percini and Lucipercini, are moderate- to large-sized species with well-developed swimbladders. Swimbladders are reduced (*Percina*) or absent in the Etheostomatini (Morgan 1936) and Romanichthyini, an adaptation common to benthic fast-stream inhabitants.

*Lateralis system* — Percids have a relatively well-developed lateralis system, although it is reduced on the head and body in some Etheostomatini. The canals on the head lie in grooves in

the underlying cranial bones. The size and shapes of the neuromasts vary from species to species (Jakubowski 1967). Species of Lucioperchinae have two supplementary lateral lines on each side of the tail (absent in the specialized genus *Romanichthys*), whereas species of Percinae either have no lateral line on the tail or else the main lateral line extends out onto the tail for a short distance. *Percina*, the most primitive genus of the Etheostomatini, has a system of uninterrupted head canals and a lateral line extending from the edge of the opercle to the hypural plate and out onto one or more scales of the caudal fin in several subgenera (Page 1977). *Ammocrypta* is similar to *Percina* but shows a reduction in some species in the number of pores in the preoperculomandibular canal from 10 to 8 or 9. There are many reductive modifications of the lateralis system within the advanced and speciose genus *Etheostoma*, as Page (1977) showed in his survey of the lateralis system of darters. Pores have been lost and canals have become interrupted in each of the four main parts of the lateralis system — body lateral line, supratemporal canal, infraorbital canal, and preoperculomandibular canal — especially in the most highly advanced subgenera such as *Hololepis* and *Microperca*, which are inhabitants of still waters.

Percids are divisible into two groups based on lateral-line structure and biology (Jakubowski 1963, 1966, 1967; Disler and Smirnov 1977; Page 1977): (1) Active pelagic predators (*Perca* and *Stizostedion*) and rheophilous benthophages (*Zingel*, *Romanichthys*, and Etheostomatini) — sight feeders with moderately developed lateral line; cephalic canals mostly enclosed in bone. (2) Benthophage dwellers of slow-flowing waters — cavernous lateral line (*Gymnocephalus* and *Percarina*); head canals strongly expanded with only narrow bony bridges over the neuromasts.

Ruffe (*Gymnocephalus cernuus*) hatch at a less-developed stage than perch and take about 7 days to reach the same level of development as newly hatched perch. Lateral-line canals are much larger in juvenile ruffe than in juvenile perch and contain more large sense organs. The external walls of ruffe head canals are membranous, providing a high directional sensitivity. Ruffe fry can feed at night, in the dark, using the lateral-line system. The neuromasts in the canals seem to be most sensitive to vibrations of low intensity, while those on the surface of the body (pit organs) are sensitive to more intense vibrations, thus acting as a defense system against predators.

*Visual apparatus* — Percids occupy a wide depth range from streams only a few centimetres deep (North American Etheostomatini) to a depth of at least 27 m for *Stizostedion vitreum vitreum* (Regier et al. 1969) and 56 m for *Perca flavescens* (Thorpe 1977b). Thus, percids are exposed to a wide variety of light intensities. Many of the shallow-living darters have pigment on the upper surfaces of their eyes that may serve as protection against the glare of the sun. Curd (1966) studied the retinal structure in 26 species of darters and found that darter retinae are generally modified for acute photopic vision. Retinae in darters are basically similar but do show some variations that are more closely associated with feeding habits than habitat. No detailed studies appear to have been published on the structure of the eyes of species of Romanichthyini.

Comparison of morphological structure and electrophysiological responses showed that the eyes of the two North American species of *Stizostedion* were similar except for the retinal epithelial pigment (REP) (Ali and Anctil 1968). Adult walleye from Ontario waters had more REP and less reflecting material than adult sauger from the same area, correlated with differences in habitat and behavior between these two species. Both species are adapted for feeding at low light intensities, the sauger particularly so. Wunder (1930) observed a correlation between the turbid nature of Balaton Lake, Hungary, and the occurrence of a reflecting layer in the eyes of *S. lucioperca*, *S. volgense*, and *G. cernuus* and Moore (1944) found the same for the walleye (*S. vitreum vitreum*). More recently, on the basis of a histological study of cone types and mosaics, Ahlbert (1970) suggested that though the Eurasian perch and pikeperch are both piscivorous, cone arrangement in the former is more adapted for movement detection, while the latter is better equipped for greater sensitivity as the bottom-dwelling ruffe is.

The reflecting material of the tapeta lucida in *Stizostedion* is a reduced pteridine, 7,8-dihydroxanthopterin, in the epithelial processes. It occurs as densely packed anisometric granules of about 0.5 mm long (Zyznar and Ali 1975). The tapetum lucidum in the sauger is not only more developed but is also more uniformly developed within the eye, whereas in the walleye it is well-developed only in the ventral region. Other structural differences suggest greater light sensitivity in the sauger. In both species, photomechanical responses to light and dark are restricted to the masking pigment (REP) and the rods. The cones are immobile (Ali and Anctil 1977). Electroretinographic determination of flicker fusion frequencies (FFF) showed that whereas in the light-adapted state there is no difference between the walleye and sauger, in the dark-adapted state

maximum values are attained at a lower light intensity in the sauger (Ali and Anctil 1977). This may be related to the greater development of the tapetum in the sauger and the consequent increase in reflectivity within its eye in comparison with the walleye.

The cones of *Stizostedion* contain multiple droplets of mitochondrial origin as in the killifish (Anctil and Ali 1976). They appear to act as light guides or funnels (Ali et al. 1977) for focusing light on the rods in the dark-adapted state. In this state, the rods are in groups optically isolated from each other by the tapetal processes. Light is reflected back and forth between the tapetal processes with additional absorption by the rods after each reflection. The passage of light through the cones and the position of the REP at the level of the cone ellipsoids limit the angle of acceptance of the cones and increase that of the rod groups — increasing sensitivity.

This mechanism is absent in *Perca*. There is no apparent difference between the retinas of *P. flavescens* and *P. fluviatilis* either in structure or in the nature of their visual pigments. In contrast to the immobile cones in *Stizostedion*, the cones in *Perca* are capable of movement (Ali and Wagner 1976) which may be related to the cones being smaller and to the absence of a tapetum lucidum in *Perca*. There is no difference between *Perca* and *Stizostedion* as far as their visual pigments, scotopic as well as photopic, are concerned. In the four species studied, the rods contain pigment based on Vitamin $A_2$ and maximally absorbing between 530 and 535 $\mu$m. The cones, which are either single or double, contain green (single) and red (both of the double) pigments. There are no blue cones. Thus, this genetically fixed factor, viz visual pigments, is the only one common to the four species.

*Central nervous system* — The external morphology of the brain in fishes of the order Perciformes is extremely varied and there are differences between families, genera, and sometimes between species. Kirka (1963) described and illustrated the brains of the eight species of percids (belonging to all three European tribes) inhabiting the Danube basin. He found that rheophilic species (*Zingel* and *Romanichthys*) have the skull depressed, the brain flattened, and the cranial cavity largely filled with brain tissue. Limnophilic species (*Stizostedion*, *Perca*, and *Gymnocephalus* spp.) have the corpus cerebelli extending vertically above the rest of the brain and the cephalic cavity is not filled by the brain to the same extent as in the rheophilic species. Similar comparative data on the North American Etheostomatini are not available. The ecological significance of gross differences in brain morphology is unknown.

## Biology

*Reproduction* — Percids are adapted to rising temperature conditions in spring and consequently have evolved an intermediate range of developmental times (i.e. compared with temperate stenotherms and eurytherms). Percids are characterized by a long, annual reproductive cycle with gonadal growth in fall and winter that culminates in spawning in spring (Hokanson 1977). Maturation occurs below 12°C and spawning occurs from late February through early July at temperatures from 3 to 26°C. A summer gonadal refractory period ensures an annual reproductive cycle. Gamete maturation, spawning, embryo and larval development, and commencement of independent feeding by larvae each have successively higher thermal requirements. Percids can adjust to different temperature regimens by shifts in their spawning season as shown by introductions into new environments (Aksiray 1961; Weatherley 1963). Spawning time of a given stock is modified only slightly by changes in temperature. Stocks adjust to accelerated thermal regimens by spawning at higher temperatures and to prolonged cold weather by spawning at colder temperatures (Rawson 1957; EIFAC 1968; Priegel 1970; Jones et al. 1977). These shifts in spawning temperature are made at the expense of gamete viability at temperature extremes (Hokanson 1977).

There is a wide variety of reproductive behavior in the Percidae. Many members of the most specialized tribe in each subfamily (Etheostomatini and Romanichthyini) develop epidermal breeding tubercles during the spawning season (Collette 1965), which facilitate maintenance of body contact between spawning pairs, especially important in moving waters where most of these species spawn. Members of the larger-sized, more generalized tribes (Percini and Luciopercini) lack these structures and usually spawn in more slowly moving waters, generally displaying little external sexual dimorphism. Males of most species of darters (Etheostomatini) are much more brightly colored than are females, especially during the spawning season. Fecundity varies from 240 to 2000 eggs averaging 1.00–2.22 mm diam in 13 species of Etheostomatini (Winn 1958a) and from 3000 to 1,185,000 eggs averaging 0.55–1.10 mm diam in the five species of European percids studied by Kryzhanovsky et al. (1953). Filuk (1962) reported the maximum fecundity of *S. lucioperca* as 2,500,000 eggs.

Darters spawn in a variety of habitats, on aquatic vegatation, in gravel, and under stones. Reproductive behavior of representative species of Etheostomatini has been summarized by Winn (1958a, b) and will not be treated further here. Balon et al. (1977) divide the Percidae into seven reproductive guilds and discuss the reproductive styles that have evolved in representatives of each guild.

*Perca fluviatilis* and *P. flavescens* spawn between February and July in the northern hemisphere and between August and October in the southern. The first females spawn earlier and at a higher temperature the lower the latitude, recorded temperatures ranging from 5 to 14°C (Thorpe 1977a). Other, local factors influence the timing of this event, for example, the occurrence of spring floods which allow perch to utilize the inundation zone of some large rivers for egg deposition. Presumably, natural selection ensures that reproduction occurs when the ensuing larvae can enter an environment with food resources sufficient for the survival of the maximum number, but critical data are lacking on this point. At the time of egg deposition, each spawning female is followed closely by several males, which shed milt close to her vent as the single, convoluted egg-strand is extruded and laced around submerged plants or debris, mostly in water 0.5–3 m deep (Fabricius 1956; Harrington 1947; Hergenrader 1969). Although defence of the eggs by the female has been observed in a tank, it is not known if this occurs regularly in the wild. The relatively unspecialized requirements for spawning substrate allow the perch to use almost all slow-moving or static waters within their geographical range. Fecundity varies strikingly between localities, egg number ranging from 950 to 210,000; egg diameter varies from 1.0 to 2.1 mm (Thorpe 1977a).

*Stizostedion lucioperca* spawns between late February and July, being earlier in lower latitudes. The thermal threshold for the beginning of pikeperch spawning is about 12°C (Deelder and Willemsen 1964; Muntian and Reznitchenko 1967). Lower temperatures, even down to 5.8°C (Bastl 1969), have been found in reservoirs south or southeast of Poland (Orava Reservoir — northern Slovakia, Volga estuary, Don estuary, Middle Dnieper, Azerbaidjan lakes). On the other hand, Brofeldt (cited by Muntian and Reznitchenko 1967) mentioned 14°C for Finnish lakes. The date of first spawning at any one locality varies between years. Local factors such as water temperature during gonad maturation (Filuk 1962; Hokanson 1977) and atmospheric pressure (Tesch 1959) influence the timing of this event. Males build nests and protect the brood: They may be monogamous. Nests are built at a depth of one to several metres, on hard bottom in the form of flat pits surrounded by a ridge of shells or gravel, generally in turbid waters, although spawning does take place in very clear water. Plant roots are, however, frequently used as substrate (Kryzhanovsky et al. 1953).

Both *S. vitreum vitreum* and *S. canadense* spawn between March and June. Spawning of walleye normally begins shortly after ice breaks up in the lake, at water temperatures of 5.6–11.1°C, and sauger often spawn immediately after the walleye. Walleye spawn at depths of 10 cm to several metres over various types of bottom in streams and lakes where there is sufficient exchange or movement of water to allow for ventilation of eggs. The two species may utilize the same areas of gravel or rubble in turbid lakes or turbid rivers. Both species have simple spawning habits; there are no redds and they broadcast their eggs with no parental care. Walleye frequently spawn in aggregations, whereas sauger and pikeperch spawn in pairs or small groups (Colby et al. 1977).

*Gymnocephalus cernuus* is an intermittent spawner (Travkina 1971) on a hard bottom of sand, clay, or gravel. The main spawning period lasts from the middle of April till June (Nolte 1939; Fedorova and Vetkasov 1974; Willemsen 1977). The maximum number of eggs may amount to 200,000 per female; the egg diameter is 0.5–1 mm (Johnsen 1965).

*Feeding* — Larger percids start feeding upon zooplankton and switch within some weeks to insect larvae and larger invertebrates. Darters (Etheostomatini) continue to feed on insect larvae and other invertebrates. The diet of the ruffe (*Gymnocephalus cernuus*) hardly changes during their lifetime: zooplankton, chironomids, oligochaetes and amphipods (Biro 1977; Willemsen 1977). The species of *Perca* and *Stizostedion* become piscivorous after different periods of time. Although piscivorous percids seem to show some preference concerning species or prey size, the wide variety in diets shows that availability of prey is more important than preference. Prey size rarely exceeds half the length of the predator and usually is considerably less. For pikeperch measuring 11–70 cm, the mean prey length amounted to 6–12 cm, whereas perch up to 40 cm consumed prey in mean length not more than 9 cm (Biro 1977; Popova and Sytina 1977; Willemsen 1977).

The diets of yellow perch and Eurasian perch are much alike: both feed on bottom inverte-

brates (chironomids, amphipods, mysids, etc.) for a rather extended period. The length at which fishes become predominant in the diet of Eurasian perch varies between 10 and 25 cm (Hartmann and Nümann 1977; Holčík 1977; Rundberg 1977; Willemsen 1977; Popova and Sytina 1977). This transition to feeding on fish may result in an increase in growth rate (Thorpe 1977a) but even when feeding mainly upon invertebrates, perch can grow extremely fast (Willemsen 1977).

Walleye prey mainly on yellow perch, and then primarily on the age-0 group, and so may considerably affect the year-class strength of the latter species (Atton and Kallemeyn unpublished data; Forney 1977; Johnson and Hale 1977; Kelso and Ward 1977; Nelson and Walburg 1977; Swenson 1977). Other fish species frequently consumed are smelt, alewife, gizzard and threadfin shad, and black crappie. Insects and crayfish sometimes form an essential part of the diet (Johnston 1977).

Sauger feed upon nearly the same species as walleye, which might lead to food competition, but according to Fitz and Holbrook (unpublished data) in Norris Reservoir that need not occur because these species tend to be concentrated at different depths.

Pikeperch start feeding upon fish at a length of 5–10 cm, depending upon the abundance of zooplankton and on the availability of prey fish (Nagięć 1977), and are then the most obligatory fish-feeding species of percid. Main prey species are cyprinids, coregonids, perch, ruffe, and smelt. In lakes where smelt is abundant, this species is the preferred food (Deelder and Willemsen 1964; Wiktor 1962; Rundberg 1977) but growth rates based upon diets of cyprinids or smelt appear to be virtually the same. After reaching a length of about 50 cm, pikeperch increase the diversity of species in their diet (Nagięć 1977; Rundberg 1977; Willemsen 1977). Although the diets of pikeperch and perch are nearly identical, food competition does not occur if food availability is high (Willemsen 1977).

Cannibalism occurs frequently among percids if food conditions are inadequate, and may then even reach a level where their own kind forms the main food resource, in many cases resulting in self-regulation of the stock (Biro 1977; Chevalier 1973; Forney 1971; Holčík 1977; Nagięć 1977; Popova and Sytina 1977).

Food consumption depends on temperature and food supply (Swenson 1977). The daily ration of predatory percids during the growing season under optimal feeding conditions amounts to about 3–7% of the body weight (Popova and Sytina 1977; Thorpe 1977a; Swenson 1977). Excess feeding at optimum temperatures results in daily rations of 11% (Willemsen 1977), whereas the daily ration for plankton-feeding perch fingerlings reaches a level of 28% (Spanovskaya and Grygorash 1977). Under good feeding conditions, pikeperch and perch consume annually at least 220% of their body weight (Popova and Sytina 1977). Evacuation rate depends strongly upon temperature, prey size, and species (Popova and Sytina 1977; Molnar et al. 1967; Schneider 1973; Swenson and Smith 1973; Thorpe 1977c).

Food conversion is temperature independent at temperatures well within the "normal" range. Rates under optimum feeding conditions vary little between species: 4–5 for pikeperch, 4–5.5 for perch (Popova and Sytina 1977; Willemsen 1977), and 4.5–6 for walleye (Swenson 1977).

Feeding activity of percids is connected with adaptation to low light intensities, often leading to two main feeding periods: early morning and evening. Pikeperch usually are inactive during daytime (Popova and Sytina 1977; Rundberg 1977). Walleye are limited in their activities by intensive light and are primarily nocturnal feeders upon pelagic prey, though they may feed at midday on demersal prey at low food densities (Swenson 1977). Sauger are still more adapted to darkness and feed in deeper water; in shallow water their activity increases with wind (Swenson 1977). Fingerlings of Eurasian perch during the plankton-feeding stage show two peaks in activity (early in the morning and in the evening) but during the benthos-feeding stage feed only in the morning (Spanovskaya and Grygorash 1977). In adult perch a frequent pattern of mid-morning and evening peaks of feeding activity may sometimes be masked, especially among piscivorous individuals, by the irregularity of prey availability (Thorpe 1977a).

*Migration* — Percids generally do not move long distances. The main pattern is migration during the period before spawning towards the spawning grounds, and after spawning, a gradual dispersion over the feeding area. Onshore spawning migrations in the spring may be guided by temperature gradients in the direction of optimal temperatures for gamete viability and embryo survival (Rawson 1957; Belyy 1963; Forney 1967; Priegel 1970). The Etheostomatini generally move upstream (or into shallower waters in lakes) for spawning and then move back downstream or into deeper waters (Winn 1958a).

Fish tagged in the spawning area are frequently recovered from the same area during a following spawning season, thus strongly suggesting the

existence of distinct spawning populations in walleye (Spangler et al. 1977) and pikeperch (Nagięć 1977). Walleye seem in many waters to be less migratory: Most tagged fish were recovered not farther away from the tagging site than 8 km (Atton and Kallemeyn unpublished data; Schupp and Macins 1977; Spangler et al. 1977), but migrations over some hundreds of kilometres are mentioned by Ferguson and Derksen (1971) and Schneider and Leach (1977) in the Great Lakes.

Migrations of yellow and Eurasian perches are also restricted (Bagenal 1977; Henking 1923; Mraz 1952; Kozikowska 1966). Although distances of 70 km can be covered, perch maintain a preference for their "own" area of the lake: Even when transported over distances of about 30 km, they showed, like pikeperch, a distinct tendency for homing (Willemsen 1977). This limited migratory behavior may even lead to different morphological groups within a lake (Chikhova 1973). Pikeperch are more migratory than perch, but despite some exceptionally long migrations of up to 82 km (Lind 1977) and 120 km (Svärdson and Molin 1973) the average migration distance does not exceed 10–20 km (Lind 1977; Rundberg 1977; Willemsen 1977).

Sauger are the most migratory of this group: Recoveries from tagged fish showed that distances up to about 380 km were covered at minimal mean swimming speeds of 19.7 km/day upstream and 21.1 km/day downstream (Fitz and Holbrook unpublished data). Vertical migration is the result of avoidance of high light intensities and low temperatures, and the presence of food and sufficient oxygen. Especially in clear water, walleye and sauger tend to stay in deeper layers at midday, but still above the thermocline (Fitz and Holbrook unpublished data; Swenson 1977; Hokanson 1977; Rundberg 1977).

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